

The University of Chicago

EFFECT OF BORON ON GROWTH
AND DEVELOPMENT OF
THE RADISH

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE
BIOLOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1941

By

JOHN SKOK

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EFFECT OF BORON ON GROWTH AND DEVELOPMENT OF THE RADISH

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 531

JOHN SKOK

(WITH FIVE FIGURES)

Introduction

AGULHON (1) found that different species of plants reacted differently toward boron, and that for each there was an optimum concentration which favored growth and yield of the plant, although he did not describe the deficiency symptoms in detail. Later HASELHOFF (14) reported that boron increased growth in beans; BRENCHLEY (3) found peas to grow better with boric acid; and MAZÉ (20) found boron was required by maize and added it to his list of essential elements. WARINGTON (29) and SOMMER and LIPMAN (28) showed definitely that boron was essential for the normal growth of the broad bean and a number of other plants. Several excellent summaries are available (4, 12, 15, 22, 33) of more recent work on this subject.

The exact role of boron is still not known. It has been possible merely to speculate as to its function by noting the development of plants when it is absent. Much has been learned from work done during the past 20 years concerning gross deficiency symptoms and histological and metabolic effects. PURVIS (24) has reviewed the effects of boron and the factors affecting its deficiency in the soil. In general, boron-deficient plants show disintegration of the meristematic and conducting tissues and the eventual death of first the growing tip and finally the entire plant, retarded root development, and brittleness of the leaf blades and petioles. EATON (8) found that the effects of boron deficiency are first noticeable in the youngest and of boron excess in the oldest portions of the plant. Some investigators (7, 21) think boron functions as a hormone or enzyme or is essential to the formation of substances which are activators or regulators of metabolic processes, while others (6, 18, 29) question the hormonal or enzymatic role. There are some indications that boron may have an effect on calcium absorption (6, 32) and utilization (19, 27); and microchemical studies by SHIVE (26) suggest that it is intimately involved in protein metabolism. Both ammonium nitrogen and sugar accumulate in minus boron plants. This strongly suggests that boron deficiency interferes with the aminization of the carbohydrate derivatives and in this way interferes with metabolic activity in meristematic regions.

In the present experiments a study was made of the effect of boron on the

growth and development of the radish. AGULHON (1) included the radish in his studies and found a definite increase in growth with boron, but he did not describe the deficiency symptoms. SHIVE (26) found definite deficiency symptoms in the Long Icicle variety 6 days after germination. The first foliage leaves became discolored and distorted, and finally the growing tips died. He did not describe symptoms of the hypocotyl or root. PURVIS and HANNA (25) found that among a number of other plants the radish showed boron deficiency symptoms in various fields in Virginia. They state that the symptoms consisted of root malformations and an internal darkening very similar to that found in turnips.

Material and methods

Seeds of *Raphanus sativus* L., variety Scarlet Globe, were planted in flats of clean quartz sand, and after 10–12 days plants of uniform size were transplanted to glazed earthenware pots filled with the same material. All plants received a minus boron nutrient until after transplanting and then received applications of the appropriate nutrient solutions every second day. The solutions were made up with distilled water and Merck's reagent quality chemicals of the following concentrations: 0.006*M* $\text{Ca}(\text{NO}_3)_2$; 0.0045*M* KH_2PO_4 ; 0.0045*M* MgSO_4 ; 0.5 p.p.m. Fe added as ferric citrate; 0.5 p.p.m. Mn added as MnCl_2 ; 0.5 p.p.m. Zn added as ZnCl_2 ; and 0.125 p.p.m. Cu added as CuCl_2 . The plus boron solution received in addition 0.5 p.p.m. B added as H_3BO_3 . The plants were harvested 39–42 days after the seeds were planted. Fresh and dry weights of the top and root portions and volumes of the root portions were taken. The volumes were determined by the water displacement method. The term root as used here includes the enlarged underground portion which consists of the hypocotyl as well as the root. Percentage dry weights and top-root ratios were also determined.

Experimentation

These experiments were of three types: (A) a study of the gross boron deficiency symptoms of the radish, (B) a study of the effect of photoperiod on the manifestation of the deficiency symptoms, and (C) a histological study.

A. GROSS BORON-DEFICIENCY SYMPTOMS

Three series of plants were grown under different treatments. The plants of series 1 received boron throughout the period of the experiment. The seeds were planted April 6, 1939, and the plants were harvested 41 days later. The plants of series 2 received boron for 18 days after planting, at which time the plants were 3–4 cm. tall and had four leaves. From then on they received a minus boron nutrient. They were planted and harvested at the same time as the plants in series 1. The plants of series 3 were grown without boron throughout the experi-

ment. They were planted May 12, 1939, and harvested 39 days later (table 1, fig. 1).

The plus boron plants of series 1 had large green leaves 15–20 cm. long and 5–6 cm. broad. The thickened portions were large, bright red, solid, and ranged from 2 to 4 cm. in diameter.

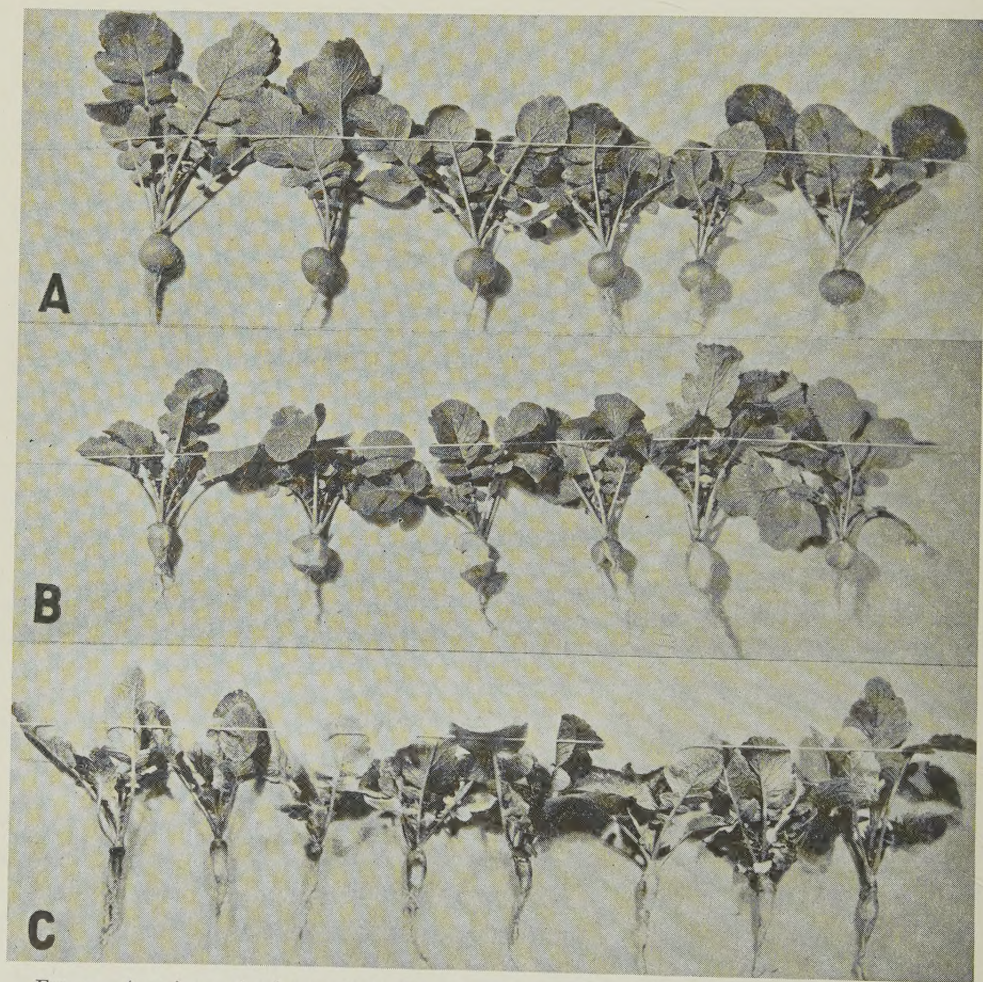


FIG. 1.—A, series 1, plus boron plants; B, series 2, plus boron for first 18 days only; C, series 3, minus boron plants.

The top portions of the plants in series 2, which received boron for the first 18 days, were well developed and similar to those in the first series, although the leaves were slightly lighter and some were distinctly mottled. The plants were also slightly smaller and the petioles were rather brittle as compared with those of the plus boron plants. The percentage dry weight was nearly the same. The

enlarged portions of this series were all light in color, and all of them were much cracked. The splitting was usually longitudinal but in some cases was also transverse. The cracks in some cases were shallow and in others were very deep; a few radishes were split almost in half. The size of the thickened portion was slightly smaller than that of the plus boron series, as is shown in table 1.

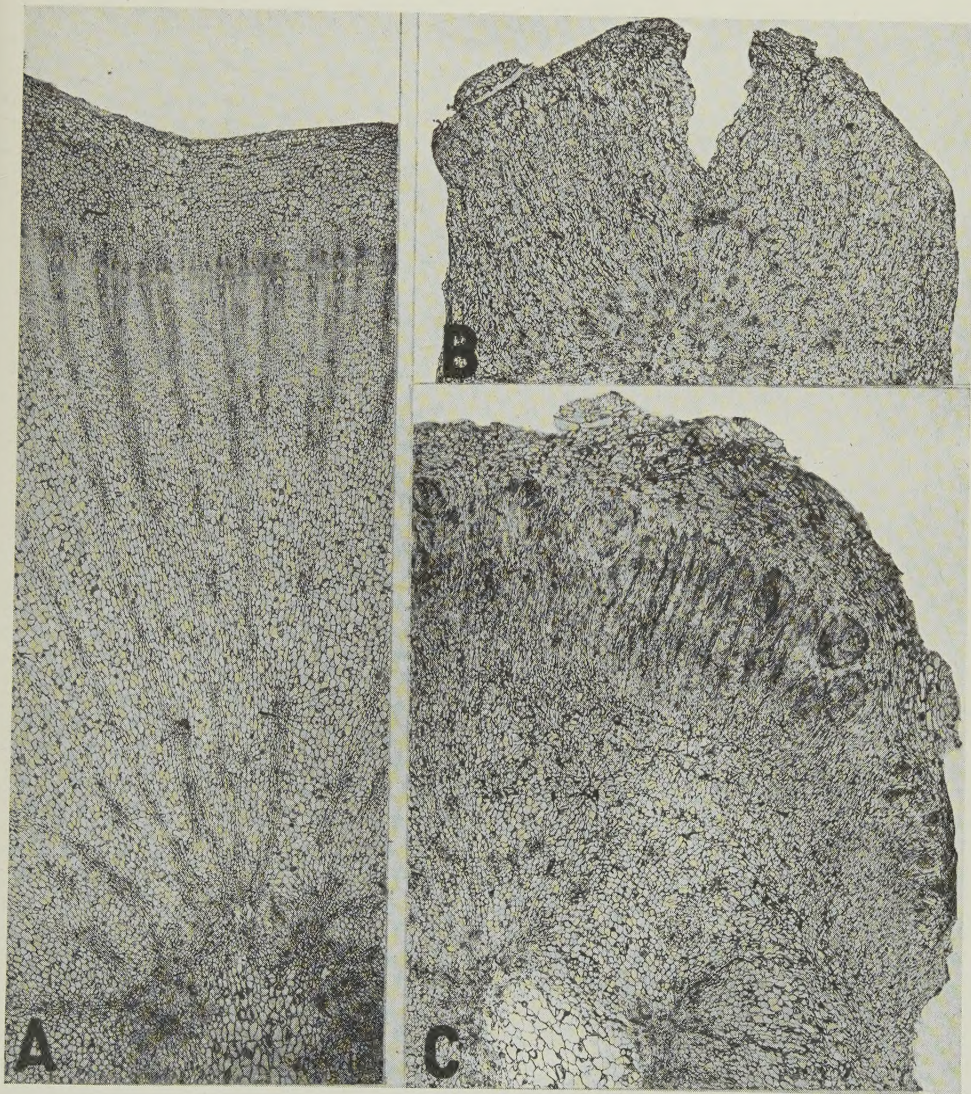


FIG. 2.—Section through hypocotyl region: *A*, plus boron; *B*, *C*, minus boron. *B* and *C* show unaffected vascular tissue at central portion of axis and absence of lignified vessels as well as of disintegrated phloem in area between central vascular tissue and cambium region. Split section (*B*) shows indistinctly developed vascular bundles, and unsplit section (*C*) shows dome arrangement of bundles at cambium region.

The plants of series 3, which were continuously on a minus boron nutrient, were much smaller than either of the other groups. The leaves were 8-15 cm. long, very pale, some extremely chlorotic, the petioles brittle and easily broken when handled. The chlorosis was confined to the areas between the veins, the veins themselves being usually green. Some of the older leaves were curled downward, but generally they were not markedly deformed. The young leaves in the center were very small, curled, thick, and usually brittle. The total growth of the tops as measured by dry weight was not much less than that in the plus boron series, but the total root growth was only about half as great. The percentage dry weight was also greater in this group than in either of the other two. The hypocotyl and

TABLE 1
DATA OF EXPERIMENTS OF PART A. VOLUMES AND WEIGHTS REPRESENT
AVERAGES PER PLANT ON 40-PLANT BASIS

CONDITION	VOLUME OF ROOT (ROOT AND HYPO- COTYL) (CC.)	WET WEIGHT		DRY WEIGHT		PERCENTAGE DRY WEIGHT			WET TOP- ROOT RATIO	DRY TOP- ROOT RATIO
		TOP (GM.)	ROOT (GM.)	TOP (GM.)	ROOT (GM.)	ENTIRE PLANT	TOPS	ROOTS		
Series 1 (plus boron)...	10.19	6.27	10.19	0.64	0.63	7.75	10.22	6.22	0.62	1.01
Series 2 (plus boron for first 18 days)	8.92	5.36	8.71	0.61	0.54	8.17	11.38	6.20	0.61	1.13
Series 3 (minus boron).	4.19	5.32	4.09	0.57	0.30	9.25	10.71	7.33	1.30	1.90

root portions of the plants in this series were much elongated, narrow, and all were nearly white in color, and split. The splitting here also was usually parallel with the axis but in some cases at right angles to it. The volumes of the thickened portions of the plants in this series were less than half of those of the plus boron series and of an entirely different shape. The volumes of the thickened portions in series 2 were only slightly smaller than those of the plus boron series, and aside from the splitting, were of about the same shape.

A common boron-deficiency symptom is death of the growing tip and cessation of further top growth. The plants in these experiments showed only moderate symptoms in the tops but marked symptoms in the underground portions. SHIVE (26) reported that lack of boron resulted in complete destruction of the growing tip in radishes grown in sand which was treated with acid. The sand used in these experiments was not so treated and may have contained minute traces of boron. The boron-deficient radishes reported by PURVIS and HANNA (25) showed symp-

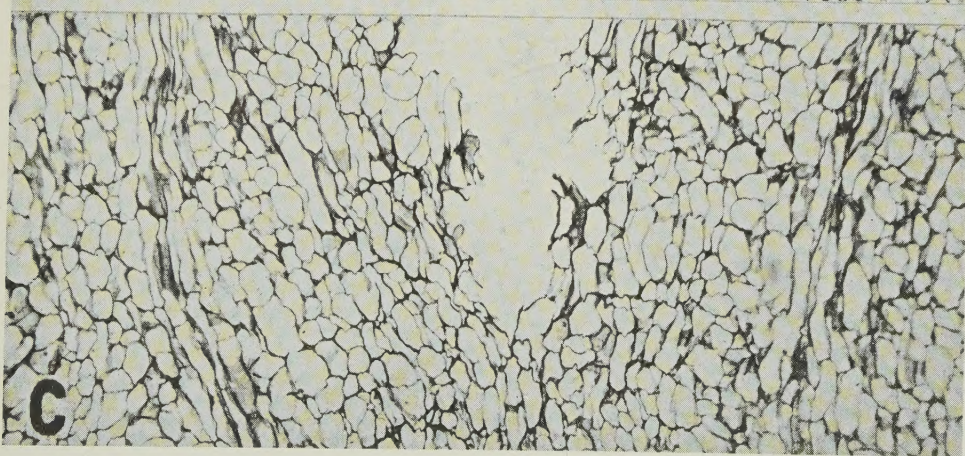
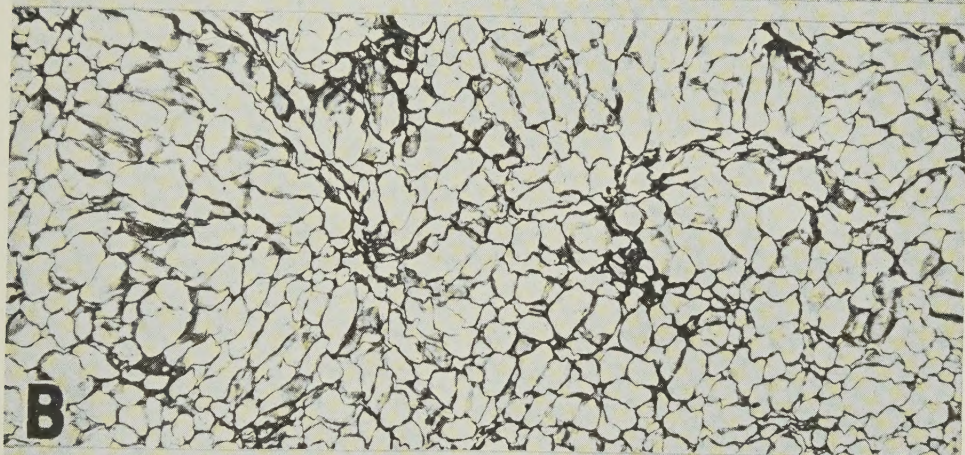
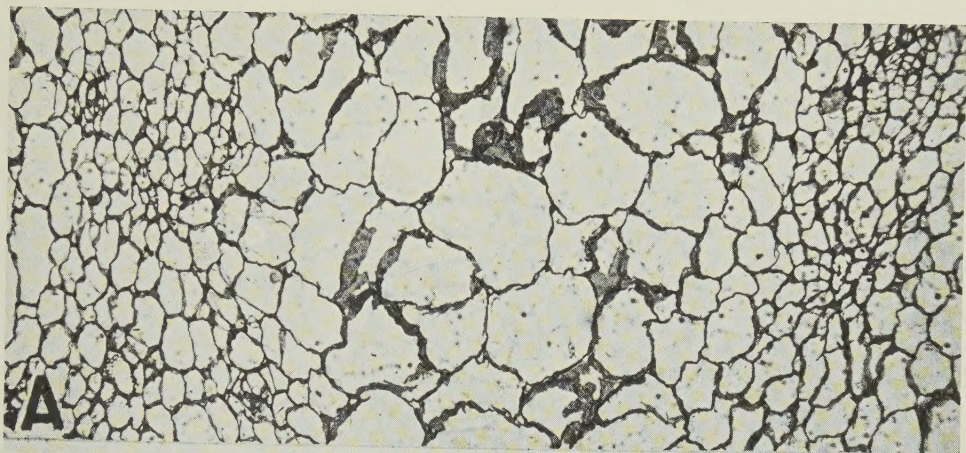


FIG. 3.—Section through hypocotyl in area between central portion of axis and cambium region: *A*, plus boron, showing vascular bundles and large xylem parenchyma cells; *B*, *C*, minus boron, showing absence of lignified vessels, disintegrated phloem cells, and smaller size of xylem parenchyma cells.

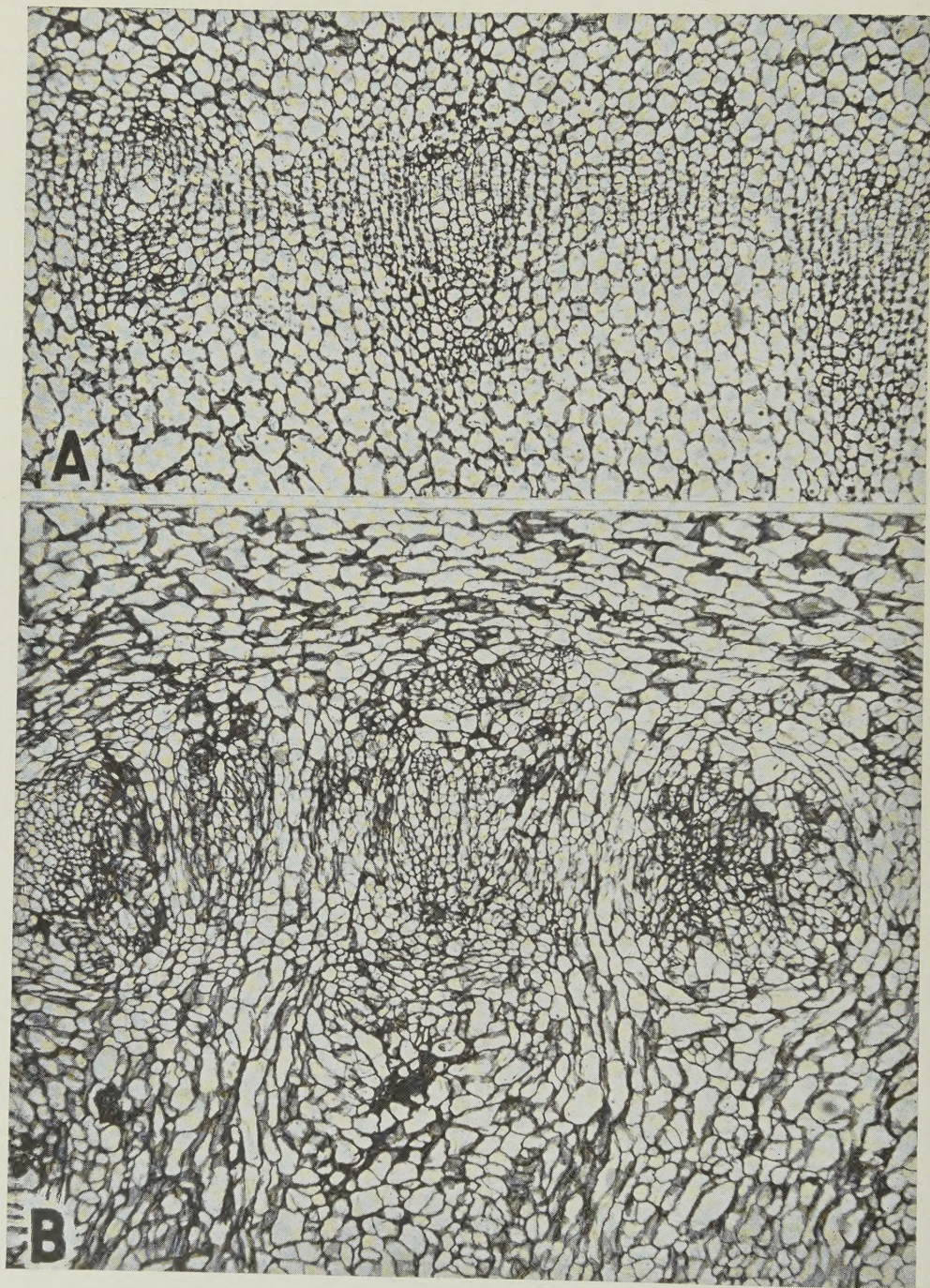


FIG. 4.—Cambium region: *A*, plus boron; *B*, unsplit portion of axis of minus boron plant showing dome arrangement of bundles and proliferation of xylem parenchyma and ray cells.

toms somewhat similar to those found in these experiments (root malformation), but they did not show any splitting. Their plants were grown in a boron-deficient soil, and possibly the deficiency was not so nearly complete. The plants of series 2, which received boron for the first 18 days, showed definite symptoms although less severe.



FIG. 5.—Cambium region of split portion of axis of minus boron plant showing indistinct vascular bundles, slightly lignified vessels, disintegrated phloem and cambium cells, and some proliferation of xylem parenchyma and ray cells.

B. EFFECT OF PHOTOPERIOD ON BORON-DEFICIENCY SYMPTOMS

Two experiments were conducted. In experiment 1 the seeds were planted May 17, 1940, and the plants harvested 42 days later. They were grown under plus and minus boron conditions; the minus boron plants received no boron throughout the experiment. One hundred and thirty plants were grown under each condition. Both boron series were grown under a short photoperiod of 7 hours (9:00 A.M. to 4:00 P.M.). Experiment 2 in this study was conducted as a check on the results of experiment 1 and on the boron-deficiency symptoms obtained in the former group of experiments, which were conducted under long photoperiod. In experiment 2 the plants were grown under the following four conditions: plus boron, long photoperiod; plus boron, short photoperiod; minus

boron, long photoperiod; minus boron, short photoperiod. The short photoperiod was also 7 hours, and the long photoperiod was the natural day length of that time (about 15 hours). The plants of experiment 2 were planted July 16, 1940, and were harvested 41 days later. Seventy plants were grown under each condition.

EXPERIMENT 1.—Under short photoperiod the boron-deficiency symptoms were not so pronounced as compared with the plus boron plants. The minus boron plants were slightly smaller and somewhat lighter in color. Their petioles were rather brittle and easily broken. The root-hypocotyl portions were smaller, more elongated, and a little lighter in color. Splitting occurred in only a few instances and in no case was so great as in the plants of the former experiments. Out of the total number of minus boron plants in this experiment, approximately 73 per cent were not split, 15 per cent had very slight splitting, and 12 per cent had more pronounced splitting (table 2).

TABLE 2
DATA OF EXPERIMENT 1, PART B. VOLUMES AND WEIGHTS REPRESENT
AVERAGES PER PLANT ON 130-PLANT BASIS

GROWN UNDER 7-HOUR PHOTOPERIOD	VOLUME OF ROOT (ROOT AND HYPO- COTYL) (CC.)	WET WEIGHT		DRY WEIGHT		PERCENTAGE DRY WEIGHT			WET TOP- ROOT RATIO	DRY TOP- ROOT RATIO
		TOP (GM.)	ROOT (GM.)	TOP (GM.)	ROOT (GM.)	ENTIRE PLANT	TOPS	ROOTS		
Plus boron.....	4.61	7.24	4.56	0.52	0.25	6.51	7.20	5.40	1.59	2.12
Minus boron....	3.31	6.20	3.28	0.47	0.18	6.90	7.57	5.63	1.89	2.54

EXPERIMENT 2.—The plus and minus boron plants grown under long photoperiod responded similarly to those in series 1 and 3 in the study of gross boron-deficiency symptoms. Thirty days after the time of planting, the tops of the long photoperiod, minus boron plants were smaller and had narrower leaves than those receiving boron. The leaves had a bluish green color, very brittle petioles, and were rather stiff and curled. At this time there was scarcely any difference between the appearance of the top portions of the plus and minus plants grown under short photoperiod. The petioles of the minus boron plants, however, were somewhat stiffer. At the time of harvesting, the long-photoperiod, plus boron plants had well-developed large green leaves and underground portions 3.5–4 cm. in diameter and bright red in color. The leaves of the minus boron plants were smaller, bluish green in color, curled, and brittle. The young leaves were deformed and also brittle. The underground portions were light in color, long, and very slender, and all were cracked. They were 5–8 cm. long and 0.5–2 cm. in diameter. The leaves of the short-photoperiod, plus boron plants were lighter in color and

smaller than those of the long-photoperiod group. The underground portions were also considerably smaller, but well formed and bright red in color. The leaves of the short-photoperiod, minus boron plants were of about the same size and color as those of the plus boron plants, but they were also brittle. The underground portions varied greatly in size, but their average was not much below that of the plus boron group. They were lighter in color and somewhat deformed and had about the same percentage of cracking as similar plants of experiment 1. The data of table 3 show that on weight and volume bases the plus and minus boron plants grown under short photoperiod made about the same amount of growth, but both groups made less growth than the minus boron plants grown under long

TABLE 3
DATA OF EXPERIMENT 2, PART B. VOLUMES AND WEIGHTS
REPRESENT AVERAGES PER PLANT ON 70-PLANT BASIS

CONDITION	VOLUME OF ROOT (ROOT AND HYPO- COTYL (CC.))	WET WEIGHT		DRY WEIGHT		PERCENTAGE DRY WEIGHT			WET TOP- ROOT RATIO	DRY TOP- ROOT RATIO
		TOP (GM.)	ROOT (GM.)	TOP (GM.)	ROOT (GM.)	ENTIRE PLANT	TOPS	ROOTS		
Plus boron, long photoperiod...	12.37	19.28	11.68	1.14	0.55	5.43	5.90	4.67	1.65	2.09
Minus boron, long photoperiod...	4.67	10.58	4.61	0.77	0.29	6.96	7.27	6.23	2.30	2.68
Plus boron, short photoperiod...	3.55	9.75	3.52	0.62	0.18	6.00	6.33	5.07	2.77	3.46
Minus boron, short photoperiod.....	3.06	9.99	3.07	0.64	0.17	6.21	6.36	5.70	3.26	3.63

photoperiod. The long-photoperiod, minus boron plants exhibited the most severe deficiency symptoms. In terms of appearance and general condition, it is evident that the plus boron plants make relatively much greater growth under long photoperiod and the minus boron plants make more growth under short photoperiod. This is probably a matter of differential rate of growth, dependent on the photoperiod, with subsequent differential nutrient requirement. The long-photoperiod plants grow more vigorously and synthesize more materials and require more nutritive substances in order to do so. If an essential element is lacking, therefore, the deficiency symptoms in such plants are more severe than in less vigorously growing plants such as those in the short-photoperiod group. This is in agreement with EATON'S (8) finding that the more vigorously growing plants exhibit more pronounced deficiency symptoms, and with those of WARINGTON (31) that the boron-deficiency symptoms of several plants were less pronounced under short than under long photoperiod.

Although the radish ordinarily flowers under long photoperiod (10, 11), only a few plants out of the entire numbers grown did so. At the same time other plants growing in the garden bloomed. This difference in the flowering response may be caused by difference in temperature or in light intensity. PLITT (23) found photo-thermal responses of the radish.

C. HISTOLOGICAL EFFECTS OF BORON DEFICIENCY

The root-hypocotyl portions of plus and minus boron plants were used in the histological study. The material was preserved in alcohol-acetic acid-formalin solution, dehydrated in an alcohol-tertiary butyl-alcohol series, imbedded, and cut at $7\ \mu$. Samples were taken at 20 days after planting and every 4 days thereafter, until time of harvesting. Any differences shown in the plus and minus boron material in the early samples were more pronounced in later stages, and for that reason photomicrographs were taken only of material collected at the time of harvesting. Slides were made of material from two different experiments (plants grown a year apart), and the histological effect of boron deficiency was found to be similar in each case. The materials for the histological study were taken from plants grown under natural long photoperiod (about 15 hours).

A number of reports have shown that boron is important in the differentiation of the vascular system, and that in its absence there is general disintegration of the cambium and phloem. AGULHON (1) noted that boron is especially abundant in lignified tissue and bark, which indicated that it may have some function in the formation of vascular tissue or the compounds which impregnate these tissues. WARINGTON (30) found that boron deficiency in *Vicia faba* caused abnormal structure of both the stem and root, the chief features being: (a) hypertrophy of the cells of the cambium followed by degeneration with discoloration, or direct disintegration of the same tissue without previous enlargement; (b) frequent disintegration of phloem and ground parenchyma; and (c) slight development of xylem and in some cases ultimate disintegration of this tissue. BRENCHLEY and THORNTON (5) found that the vascular bundles related to the nodules on the roots of *Vicia faba* either failed to develop entirely or only to a small extent when boron was lacking. Anatomical studies on the tomato by JOHNSTON and DORE (16, 17) and by FISHER (9) showed disintegration of the phloem of the petioles and stems of boron-deficient plants. The total sugars and starch were more abundant in the leaves of the minus boron than in the plus boron plants. This was thought to be caused by injury to the conductive tissues, which reduced their capacity to translocate sugars. HAAS and KLOTZ (13) found boron to be essential for cell division in meristematic tissue of growing points such as buds, and equally essential for cambial activity. They found that the cambium and phloem disintegrated in minus boron citrus plants. The xylem was affected to a less extent. They also

found that sugar accumulated in the leaves of the affected plants because of the disintegrated conducting system, and that upon the addition of boron to these cultures there was rapid growth of new conductive tissue followed by decrease in the sugar content of the leaves.

CHANDLER (2) studied boron deficiency in eleven species of *Brassica*. In boron-deficient broccoli and Brussels sprouts he found that cell division stopped in the root tips and the root cap disintegrated. In rutabaga he observed crushing of meristematic cells of the stem tip, and in the root he found crushing of cortical cells, accumulation of cell inclusions in xylem parenchyma cells, elongation of certain cells near the cambium, and failure of the cork cambium to form cork. He also found crushing of cells in the cortex of the stem of cabbage, and when leaf blades of these boron-deficient plants were cut a cork cambium did not develop, but with similar treatment to plants supplied with boron, a cork cambium developed and healing occurred.

The effects of boron deficiency on the structure of the radish are somewhat similar to those in the preceding plants in that the vascular tissues are affected rather markedly. Sections through the hypocotyl of plus and minus boron plants show the general structure and the tissues affected by the deficiency (fig. 2). The vascular tissue near the center of the axis, including the primary tissue, was not affected. This is the first differentiated vascular tissue, and small amounts of boron may have been present from the seed or as impurities in the chemicals and sand, at the time of its maturation. After this amount of boron is exhausted the vascular tissue developing later would be lacking an element necessary for its development. Injurious effects on this later-forming vascular tissue again indicate that boron cannot be reutilized but that a continuous supply is necessary.

The vascular tissues occupying the area between the central, first formed, uninjured vascular tissue and the outer cambium region were markedly affected (fig. 3). Normally developed and lignified vessels in this area were entirely absent. The phloem cells disintegrated and left dead, dark-staining areas. The xylem parenchyma cells appeared to be uninjured and in some cases even rather active. The size of the xylem parenchyma cells of the boron-deficient radishes was generally smaller than those of the plus boron plants. Actual disintegration of these cells, as in the case of the ground parenchyma of *Vicia faba* reported by WARINGTON (30), was not observed.

The cambium region is of particular interest in that it shows a dual response (fig. 2). Axes which were cracked had very slightly developed vascular bundles in the cambium region near the cracks (fig. 5). Some disintegration of phloem also took place but not to the same extent as in the deeper areas. Well-developed vessels were almost entirely lacking, but some small, thin-walled vessels were

present. The cambium cells were almost entirely disintegrated. The xylem parenchyma, and particularly the ray cells, were rather active and showed proliferation.

The cambium region of axes which were not deeply cracked had an entirely different structure (fig. 4). The vascular bundles were fairly well developed and were arranged in pronounced domes and circular areas. A few vessels were present in these bundles, but they were rather thin walled, smaller, and much less lignified as compared with those of the plus boron sections. There was no pronounced phloem or cambium disintegration in these bundles, but the tissues were rather poorly developed and indistinct. Again the xylem parenchyma and particularly the ray cells were highly active. In some cases the proliferated ray cells formed complete rings around the bundles. Both these responses of the cambium region may be seen in the same axis, in which case the former is present at or near a crack and the latter where no splitting has taken place (fig. 2C).

These histological observations suggest that the splitting of the radish is a result of the failure of normal vascular tissue development, coupled with differential growth pressure. The lack of lignified xylem development and the areas of dead phloem create weak regions where the splitting may occur. The cessation of cambial growth, together with active xylem parenchyma and ray cells inside the cambium, result in internal pressure because of this unequal growth.

Summary

1. Radish plants deficient in boron produced small leaves with light bluish green color, which were (especially the petioles) brittle and curled down. The thickened underground portions were light in color, narrow and elongated, and severely cracked.

2. When boron was added up to 18 days after planting and then withheld, the top portion made greater growth but the brittleness of the leaves and the light color of the foliage were still apparent. The enlarged underground portion attained greater size and more normal shape but was also cracked.

3. Under short photoperiod the boron-deficiency symptoms were much less pronounced. Splitting of the underground portion was present in only about 27 per cent of the minus boron plants.

4. The vascular tissue near the center of the axis was not affected by boron deficiency.

5. Normally developed and lignified vessels in the area between the central, unaffected vascular tissue and the outer cambium region were entirely absent, and the phloem cells in this region had disintegrated.

6. The cambium region, if located at or near a crack, had slightly developed vascular bundles. The cambium and phloem cells were mostly disintegrated, and

well-developed vessels were lacking. The xylem parenchyma and ray cells were rather active.

7. The cambium region, if not located near a crack, had well-developed vascular bundles arranged in pronounced domes and circular areas. The vessels were unglified, but there was no pronounced phloem or cambium disintegration. The xylem parenchyma and ray cells were here also highly active.

8. The splitting is caused by the failure of normal vascular tissue development, coupled with differential growth pressure.

The writer wishes to express his sincere thanks to members of the department of botany at the University of Chicago for their kind help and valuable suggestions made during the course of this work.

DEPARTMENT OF BOTANY
UNIVERSITY OF CHICAGO

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